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Effects of alien plant management and fire on soil seed banks and regeneration in the Cape Peninsula National Park, South Africa

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The regeneration of alien and indigenous vegetation in various post-fire environments, following the extensive January 2000 wildfires on the Cape Peninsula, South Africa, is described. The effects of dry season wildfire burning of standing alien plants and stacks of mechanically cleared, alien plant material, on post-fire seed banks and vegetation recovery, are presented. These are compared to the effects of wildfire burning on adjacent stands of un-invaded Sandstone Fynbos (previously known as Mountain Fynbos) vegetation and to that on cleared areas surrounding wildfire burnt stacks. The effects of stacking and controlled burning of slash of cleared alien plant material on regeneration potential, under cool weather conditions, are also reported. Seed banks and regeneration were linked to pre-fire vegetation characteristics, fire intensity and, in particular, to the management of alien plants. Large volumes of either standing or stacked alien woody plant biomass impact negatively upon post-wildfire seed banks and upon the recruitment of indigenous fynbos vegetation. Heat damage, associated with stacks of woody alien biomass, kills all seeds to a soil depth of at least 0.15m. In contrast, the controlled winter burning of stacks of alien material results in large scale localised germination of alien seeds. Both persistent indigenous seed banks and the seed of alien invasive species are present in the burnt disturbed areas surrounding stacks of alien slash burnt in wildfires. It is concluded that the current practice of stacking slash resulting from the control of alien plants requires urgent review.

Introduction

In South Africa, the control of alien plant species poses ecosystem managers with their biggest problem in terms of manpower, money and time spent (Marais 1998). Woody alien plants have also altered fire regimes in the Fynbos Biome, producing exceptionally intense fires with suggested negative effects on the regeneration of the indigenous vegetation (Van Wilgen and Richardson 1985, Richardson and Van Wilgen 1986, Holmes and Cowling 1997a, Scott *et al*. 2000).

Alien vegetation management in the greater Cape Peninsula National Park, a reserve situated in the South African fynbos shrublands, currently requires that felled alien vegetation be stacked, leaving the piles scattered through the landscape (hereafter these will be referred to as stacks) (Milton and Hall 1981, Holmes *et al*. 1987, Macdonald *et al.* 1989, Euston-Brown 2001). Stacking has merit in that seeds of serotinous alien species are concentrated beneath the stacks (this has advantages for future control), access into cleared sites is improved (for follow-up eradication) and the activities of entrepreneurial wood collectors are concentrated in the vicinity of the stacks. However, it has been suggested that fires burn stacks at highly elevated temperatures, killing soil-stored indigenous and alien seeds. This results in the formation of so-called heat scars on the landscape (Richardson and Van Wilgen 1986, Breytenbach 1989, Macdonald *et al.* 1989, Holmes *et al*. 2000, Euston-Brown 2001).

The Cape Peninsula was subjected to extensive accidental wildfires during the dry season in January 2000. Fire line intensities were extremely high and are estimated to have reached 10 000–40 000kW m^{-1} (Scott *et al.* 2000). Areas with dense woody alien vegetation had far higher fuel loads than un-invaded fynbos vegetation and were subjected to the hottest fires (Scott *et al.* 2000, Euston-Brown 2001). Of the total burned area, 26% had been subjected to clearing activity in the two years prior to the fire (Scott *et al.* 2000). In these cleared areas, slashed and stacked alien vegetation subsequently formed heat scars (Scott *et al.* 2000).

Holmes and Cowling (1997a) state that 'information is needed urgently on what remains in the seed banks of invaded fynbos shrublands and how this translates to restoration potential for these sites', while Holmes and Cowling (1997b) add that: 'further studies are required to establish the depth distribution of fynbos seeds in invaded and un-invaded stands'. Indigenous species with soil-stored seed banks are especially important in contributing to community richness and diversity (Holmes and Cowling 1997b, Holmes *et al.* 2000, Holmes 2002) and form the dominant plant cover in many un-invaded Mountain Fynbos areas (Kruger 1979). Intermittent fire kills many fynbos species, which then regenerate largely from soil-stored seed banks, although serotiny is common among overstorey dominants (Kruger and Bigalke 1984, Pierce 1987, Holmes and Cowling 1997b). Fynbos shrublands are thus largely dependent on soil seed banks for recruitment after fire (Le Maitre and Midgley 1992).

In this study, post-fire depth and seed size distribution of indigenous and alien seed are examined in various invaded and un-invaded areas. Post-wildfire and controlled winter burning effects of stacking are quantified, as are the effects of wildfire in a standing mature woody alien stand and in un-invaded fynbos.

Materials and Methods

In order to monitor regeneration patterns and to infer viable seed-bank and propagule sizes (Roberts 1981), adjacent field plots were selected in the Silvermine Valley, Cape Peninsula National Park, during February 2000. Sites had the following characteristics:

1. Wildfire burnt standing aliens (principally *Acacia longifolia*, *Hakea drupacea* [formerly *H. suaveolens*] and *Pinus pinaster*);
2. Wildfire burnt Sandstone Fynbos (previously known as Mountain Fynbos (Mucina and Rutherford 2004));
3. Wildfire burnt stacked aliens (heat scars) (principally *Acacia cyclops*, *A. longifolia*, *A. saligna* and *Pinus pinaster*);
4. Burnt cleared areas surrounding stacks (previously *Acacia cyclops*, *A. longifolia*, *A. saligna* and *Pinus pinaster*) and
5. Control burnt stacks (principally *A. saligna* but including *Acacia cyclops*, *A. longifolia* and *Pinus pinaster*).

All invaded stands were dense with a long history of invasion, although the dates of invasion were not available. Field trials to assess the regeneration of vegetation and to obtain samples for greenhouse germination trials had the following designs:

1. Burnt Sandstone Fynbos and burnt standing alien vegetation. Five, randomly placed, 5m x 5m primary plots with four 1m x 1m subplots located at each corner of the larger plot;
2. Burnt stacks and adjacent burnt cleared areas: One 2m x 2m primary plot in each of five burnt stacks with one 1m x 1m subplot in the southeast corner. Five similar plots were situated in the adjacent burnt cleared area. Plots in the stacks were reduced in size in order to minimise edge effects.

Abundances of the following regeneration guilds were determined in all primary field plots: woody alien reseeders; woody alien resprouters; indigenous reseeders; woody indigenous resprouters; herbaceous indigenous resprouters (excluding hemicryptophytes); resprouting hemicryptophytes (hereafter referred to as tussocks) and geophytes. The term ‘reseeders’ is used here to refer to obligate seeders. Morpho-species richness of each guild was also recorded in each 1m x 1m plot (morpho-species are plant taxa recorded as being distinct based on morphological differences observed in the field). Counts were conducted in (1) the burnt standing alien and (2) burnt Sandstone Fynbos vegetation types in February, March, April, May, June and September 2000 and in January 2001. Counts in (3) wildfire burnt stacks (heat scars) and (4) the burnt cleared areas were conducted in April and September 2000 and again in January 2001. In April 2001, additional field plots were selected where an alien stand (predominantly *A. saligna*) had been mechanically cleared and the slash stacked. These stacks had been deliberately control-burnt under cool weather conditions in June 2000. (5) Five control burnt stacks were randomly selected with a single 2m x 2m plot centred in each of them. Counts of individuals and morpho-species were made in May 2001.

The following sampling and seedling emergence techniques were used to infer post-fire soil seed bank sizes. During March 2000, soil was collected from burnt fynbos; burnt standing alien; wildfire burnt stacks and burnt cleared area sites. Four blocks of soil (25cm x 25cm) were removed, using a garden spade, immediately outside each 5m x 5m plot (burnt standing alien and burnt fynbos habitats) to avoid disturbance within the monitoring plot (Roberts 1981). Each sample was made up of three sub-samples collected from three depth intervals, viz. 0.00–0.02m, 0.02–0.05m and 0.05–0.15m below the surface. The four samples taken from outside each 5m x 5m plot were then bulked into their respective depth classes and mixed.

The heat scar and burnt cleared area samples necessitated a different procedure due to limited glasshouse space. One soil sample (made up of three sub-samples from the same three soil depths as with the burnt standing alien and burnt fynbos habitats) was collected from the centre of each of five heat scars while five similar samples were collected from the surrounding burnt cleared area. The heat scar sub-samples arising from each of these five plots were then bulked to form one sample for each depth, viz. three samples. The same procedure was followed for samples collected from burnt cleared areas.

Each bulked depth sample was then sifted into four particle size classes (2–8mm, 1 000µm–2mm, 425–1 000µm and <425µm) to investigate the size distribution of seeds within the soil profile. After sifting, measured volumes of soil (arising from each site, depth and size class combination) were planted out in flat seedling trays (57mm x 127mm) on a layer of ‘fynbos soil mix’, obtained from the National Botanical Institute, Kirstenbosch. This soil was used, as it is sterile of additional seed. Four additional control trays containing only ‘fynbos soil mix’ were prepared to serve as substrate and seed contamination controls. All the trays were stored dry for approximately two and a half months at ambient temperatures until the onset of the rainy season (June 2000) in the study area (De Villiers *et al*. 1993).

The trays were then placed in a glasshouse at the Botanical Gardens, University of Stellenbosch. The glasshouse has ventilated sides, which enables diurnal temperature fluctuation, a necessary germination cue in some taxa (Roberts 1981, Brits 1986, Pierce and Cowling 1991, Pierce and Moll 1994). The ventilated sides also ensure air movement, essential for optimal germination. A micro jet system was used to irrigate the trays from June 2000 to June 2001. The trays were also shifted intermittently in a random pattern in an attempt to homogenise growing conditions. Emergent seedlings were counted on 2 June 2000, 20 June 2000, 26 July 2000, 1 September 2000, 18 October 2000, 18 January 2001 and during May 2001. All new seedlings counted on these dates were marked with coloured toothpicks. Upon flowering, seedlings were removed for identification and most duplicates were removed on 18 October 2000 to provide the remaining plants with additional growing space.

Mann-Whitney U-tests were used to compare seedling counts in wildfire burnt fynbos vs wildfire burn alien treatments. Wildfire burnt cleared and burnt stack sites were not included in statistical analyses due to insufficient replication as a result of design constraints. Kruskal-Wallis tests were applied to comparisons of propagules per regeneration guild between sites.

Results

Field regeneration

Field abundance and diversity (m^{-2}) of all seven regeneration guilds differed significantly in response to invasion, clearing, stacking and associated fire temperatures. Total counts of indigenous propagules were highest in burnt fynbos plots, followed by control burnt stacks, burnt cleared areas, burnt standing aliens and lowest in wildfire burnt stacks, in that order (Tables 1 and 2). Conversely, counts of woody alien seedlings were highest in control burnt stacks, followed by burnt standing aliens, burnt cleared areas, burnt fynbos plots and wildfire burnt stacks in that order (Tables 1 and 2). Morpho-species diversity counts resulted in similar significant trends (Table 3). One year after the fire, indigenous species richness in the burnt cleared areas (11.80m^{-2}) approximated that of un-invaded burnt fynbos (12.30m^{-2}). Indigenous morpho-species diversity at this stage was 3.90m^{-2} in control burnt stacks, 1.65m^{-2} in burnt standing aliens and the lowest in heat scars, viz. 0.85m^{-2} (Table 3).

Regeneration of geophytes and tussocks were both significantly reduced in numbers in the wildfire alien standing burnt and wildfire alien stacked areas. Additionally, the geophytes appeared to have been negatively affected by dense stands of aliens prior to fires, as the burnt cleared alien fynbos vegetation was also low in geophytes compared to uninvaded burnt fynbos (Table 1).

In the field, most guilds reached maximum abundance levels by September 2000 while some peaked in January 2001 (Tables 1 and 2). January 2001 was also the month when regenerating propagules in the control burnt areas were enumerated. September 2000 and January 2001 data are thus presented here in tabular form (Tables 1 and 2).

Seed banks — treatment effects (greenhouse germination trial)

The greenhouse germination trial exhibited differences in soil seed bank abundance and richness in response to inva-

Table 1: Mean abundance of regenerating individuals per m^2 in post-fire sites in September 2000

Regeneration guild	Density (m^{-2})				H	P
	Wildfire burnt fynbos	Wildfire burnt standing alien	Wildfire burnt alien cleared fynbos	Wildfire burnt burnt alien stacks		
Indigenous seedlings	140.2 (30.9)	2.8 (1.81)	84.3 (14.6)	1.7 (0.5)	15.2	0.0016
Alien seedlings	2.0 (0.8)	35.3 (9.58)	47.0 (13.3)	1.9 (1.6)	13.9	0.0030
Alien resprouters	0	0	1.1 (0.4)	0	14.1	0.0028
Tussocks	39.4 (11.9)	0	25.8 (7.0)	0.1 (0.1)	15.9	0.0012
Geophytes	35.5 (10.1)	0	8.2 (3.5)	0.2 (0.1)	17.2	0.0007
Herbaceous resprouters	7.0 (2.2)	0.2 (0.1)	1.5 (1.5)	0.2 (0.1)	10.2	0.0170
Woody resprouters	1.6 (0.9)	0.2 (0.1)	0.3 (0.2)	0	7.0	0.0713
Total propagules	225.5 (37.4)	38.3 (10.0)	168.0 (22.5)	3.9 (1.5)	16.2	0.0011

Figures in parentheses indicate standard errors of the means (n = 5)
Multiple Comparisons of the mean ranks for all guilds were calculated using the Kruskal-Wallis test (df = 3, n = 20). H = test statistic

Table 2: Mean abundance of regenerating individuals per m^2 in post-fire sites in January 2001

Regeneration guild	Density (m^{-2})					H	P
	Wildfire burnt fynbos	Wildfire burnt standing alien	Wildfire burnt alien cleared fynbos	Wildfire burnt stacks	Control burnt alien stacks		
Indigenous seedlings	37.3 (6.8)	4.5 (1.8)	58.7 (17.8)	1.4 (0.6)	86.9 (7.4)	20.3	0.0004
Alien seedlings	2.2 (0.9)	31.6 (10.9)	22.1 (3.1)	1.6 (1.1)	504.3 (90.0)	20.3	0.0004
Alien resprouters	0	0	1.1 (0.4)	0	0	18.1	0.0012
Tussocks	33.9 (13.2)	0	19.4 (7.1)	0	0	22.2	0.0002
Geophytes	4.0 (3.2)	0	0.8 (0.3)	0	0	16.2	0.0027
Herbaceous resprouters	6.6 (2.2)	0.6 (0.3)	0	0.2 (0.1)	0	18.3	0.0011
Woody resprouters	5.4 (2.8)	0.6 (0.4)	0.2 (0.2)	0	0	16.9	0.0021
Total propagules	89.3 (19.6)	37.3 (10.4)	102.1 (20.6)	3.05 (1.0)	591.2 (96.4)	20.9	0.0003

Figures in parentheses indicate standard errors of the means (n = 5)
Multiple Comparisons of the mean ranks for all guilds were calculated using the Kruskal-Wallis test (df = 4, n = 25). H = test statistic

sion, clearing, stacking and, by implication, associated fire temperatures. While the mean total numbers of indigenous seedlings (± standard errors) was similar in soil from the fynbos (22.70 ± 5.12) and cleared areas (26.76), native seed germination was considerably lower in soil collected from under the burnt standing aliens (2.92 ± 0.95, and significantly different to fynbos sites, U = 0, P = 0.0079) and wildfire burnt stacks (1.11) (Figure 1). One fynbos sample was an outlier (0.05–0.15m depth and 1 000µm–2mm size) containing approximately 1 595 seedlings per litre of soil, most of which were an unidentified *Erica* species. This is likely the result of the sample being located under one or more parent plants prior to the fire or ant dispersal (myrmecochory). Results and discussions hereafter exclude this outlier.

Few woody alien seedlings germinated in the greenhouse germination trial but fewer germinated in wildfire burnt stack soils (0.83), burnt fynbos soils (1.60 ± 1.60) and burnt standing alien vegetation soils (2.02 ± 1.29, i.e. no significant difference compared to fynbos sites, U = 11, P = 0.8413), than in burnt cleared area soils (2.50) in that order (Figure 1).

Seed banks — soil depth effects (greenhouse germination trial)

In soils from under burnt fynbos, most indigenous seedlings (including species such as, *Erica hirtiflora*, *Metalasia muricata* and *Diascia elongata*) and a single *A. saligna* seedling, germinated from 0.02–0.05m soil depth (Table 4). The majority of indigenous seedlings in fynbos soils also regenerated from the intermediate particle size classes (surrogate for seed size), namely the 1 000µm–2mm and 425–1 000µm particle size classes (Tables 5 and 6). Similar patterns were evident in burnt cleared area soils where the majority of indigenous seedlings (including *Erepsia anceps* and *Pelargonium chamaedryfolium*) germinated from a slightly deeper depth class (0.05–0.15m depth) while four *A. cyclops* seedlings germinated from the 0.02–0.05m soil depth (Table 4).

The majority of indigenous seedlings were also counted from the intermediate particle size classes (1 000µm–2mm and 425–1 000µm) in the burnt cleared area trays (Table 5). Appreciable germination also occurred in soils from 0.02–0.05m depth (1 000µm–2mm and 425–1 000µm particle size) in these areas (Table 6). In soils from under burnt standing aliens, the majority of alien seedlings germinated from 0.02–0.05m depth, while most indigenous seedlings (including *Erica phylicifolia*) germinated from the deepest (0.05–0.15m) soil layers, many being small-seeded species (Tables 5 and 6). The alien seeds were also larger (Table 5). Very few seedlings germinated from soil under the wildfire burnt stacks soils irrespective of particle size or depth of burial (Tables 4, 5 and 6). One *A. cyclops* seedling germinated from 0.02–0.05m soil depth, two *Lobelia* sp. seedlings and two *Lepidium pinnatum* seedlings germinated from 0.00–0.02m soil depth (Table 4). A total of 43 species were recorded in the fynbos soils, 20 in burnt standing alien soils, 15 in burnt cleared area soils and four in heat scar soils. A comparison of seedlings per litre in wildfire burnt fynbos versus wildfire burnt alien sites yielded no significant differences in the largest seed sizes at all depths, although there were significant differences in numbers of seedlings from intermediate seed sizes at all depths (Table 6).

Discussion

Post-fire field counts of regenerating guilds undertaken during 2000 and 2001 showed that invasion by woody alien plants, whether under burnt standing aliens, burnt cleared areas or under burnt stacked materials, influenced the

Table 3: Mean species richness m^{-2} in post-fire sites in September 2000 and January 2001

Regeneration guild	Species richness per treatment (m^{-2})							H	P
	Wildfire burnt fynbos Sep 2000	Wildfire burnt standing alien Sep 2000	Wildfire burnt fynbos Jan 2001	Wildfire burnt standing alien Jan 2001	Wildfire burnt cleared Jan 2001	Wildfire burnt stacks Jan 2001	Control burnt stacks Jan 2001		
Indigenous seedlings	12.0 (0.4)	1.1 (0.4)	7.6 (0.5)	1.4 (0.2)	9.3 (0.5)	0.8 (0.2)	3.9 (0.2)	31.2	0.0000
Alien seedlings	0.6 (0.18)	2.0 (0.2)	0.8 (0.1)	1.8 (0.2)	1.2 (0.10)	0.4 (0.2)	1.0 (0.0)	27.3	0.0001
Alien resprouters	0	0	0	0	0.2 (0.2)	0	0	12.4	0.5454
Tussocks	2.8 (0.5)	0	2.8 (0.5)	0	2.1 (0.5)	0	0	31.0	0.0000
Geophytes	3.7 (0.2)	0	0.6 (0.2)	0	0.4 (0.1)	0	0	28.9	0.0001
Herbaceous resprouters	1.0 (0.1)	0.2 (0.1)	0.9 (0.1)	0.2 (0.1)	0	0.1 (0.1)	0	27.1	0.0001
Woody resprouters	0.5 (0.2)	0.2 (0.1)	0.5 (0.2)	0.2 (0.1)	0.1 (0.1)	0	0	17.6	0.0073
Indigenous richness	19.9	1.4	12.3	1.7	11.8	0.9	3.9	30.8	0.0000
Total richness	20.5	3.3	13.1	3.4	13.2	1.3	4.9	31.8	0.0000

Figures in parentheses indicate standard errors of the means (n = 5)
Multiple Comparisons of the mean ranks for all guilds were calculated using the Kruskal-Wallis test (df = 6, n = 35). H = test statistic

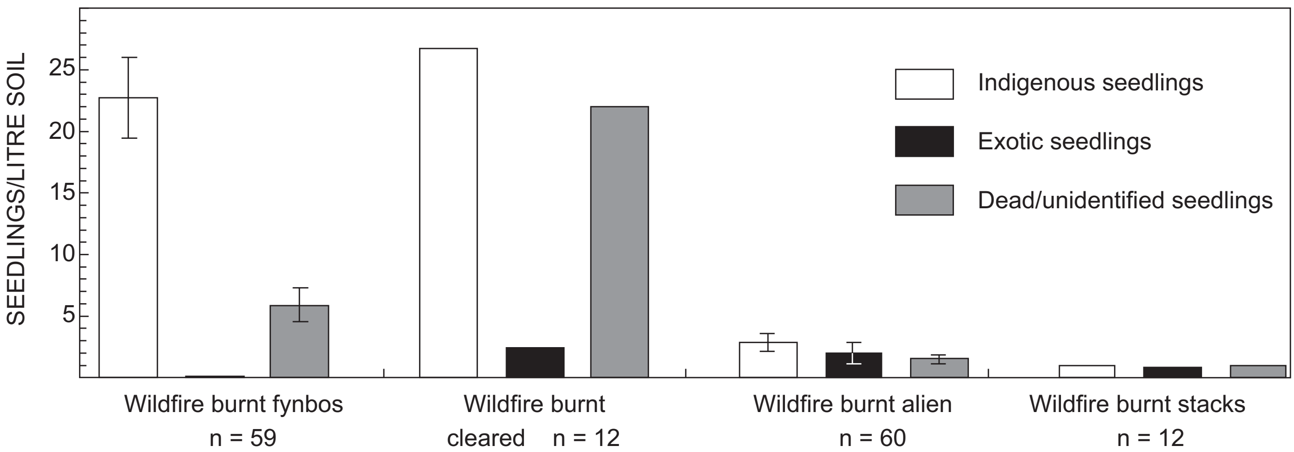

Figure 1: Total numbers of indigenous, alien and dead/unidentified seedlings regenerating per litre of soil from different post-fire sites. Error bars indicate standard errors of the means. Mann-Whitney U-test comparisons between wildfire burnt fynbos and wildfire burnt alien treatments: indigenous seedlings, U = 0, P = 0.0079; alien seedlings, U = 11, P = 0.8413; unidentified seedlings, U = 2, P = 0.0317

Table 4: Depth distribution of seedlings per litre of soil from different post-fire treatments

Treatments	Soil depth	Indigenous seedlings	Alien seedlings	Dead/Unidentified seedlings
Wildfire burnt fynbos	0.00–0.02m	20.0 (6.5)	0	3.4 (1.2)
	0.02–0.05m	34.3 (8.1)	1.6 (1.6)	10.4 (3.8)
	0.05–0.15m	13.1 (3.0)	0	3.8 (1.5)
Wildfire burnt standing alien	0.00–0.02m	1.5 (0.5)	0.7 (0.7)	0.4 (0.2)
	0.02–0.05m	1.2 (0.9)	4.2 (2.7)	2.0 (0.3)
	0.05–0.15m	6.0 (2.1)	1.2 (1.2)	2.4 (1.1)
	H	22.8	4.5	10.6
	P	0.0004	0.4747	0.0607
Wildfire burnt alien cleared fynbos	0.00–0.02m	7.8	2.5	14.4
	0.02–0.05m	18.9	5.0	27.8
	0.05–0.15m	53.6	0	23.6
Wildfire burnt alien stacks	0.00–0.02m	3.3	0	3.3
	0.02–0.05m	0	2.5	0
	0.05–0.15m	0	0	0

Figures in parentheses indicate standard errors of the means
Multiple Comparisons of the mean ranks for all seedling types in wildfire burnt fynbos vs wildfire burnt alien sites were calculated using the Kruskal-Wallis test (df = 5, n = 30). H = test statistic

regeneration patterns of indigenous and alien propagules. Alien woody plant invasions, the management techniques applied and the associated altered fire characteristics affect the total number of regenerating individuals and species diversity.

A paucity of indigenous propagules, probably as a result of the high fire intensities in the areas with burnt standing alien infestations, is conspicuous, while the post-fire dominance of alien species has shifted from two dominant species (*Hakea drupacea*, *Pinus pinaster*) to a mixture of five woody alien species (*A. cyclops*, *A. longifolia*, *A. saligna*, *Hakea sericea* and *H. drupacea*). Alien seeds in this site were either better adapted to higher fire intensities than their indigenous counterparts (Jeffery *et al.* 1988), or large pre-fire seed stores and high viability resulted in their post-fire dominance (Richardson and Van Wilgen 1984, Holmes 1987, Manders 1990, Holmes and Cowling 1997a). Indigenous seeds, which escaped the fire in these areas, may also have been buried too deeply and/or their seed sizes were too small for in-field germination, confirming similar observations by Bond *et al.* (1999).

Control burning of stacks under cool weather conditions produced the anticipated result, viz. large-scale regeneration of woody leguminous alien plants. While effective in removing alien biomass after felling, the resulting propagules have to be pulled or sprayed within a year of burning before plants mature and produce more seed. Pulling can however disturb the soil and potentially damage indigenous seedlings already present or bring new ungerminated alien seed to the surface for a second flush of germination. Furthermore, stacking does not concentrate seeds of non-serotinous species and thus the surrounding unburnt areas retain their large ungerminated soil-borne alien seed store (Holmes and Cowling 1997a). Winter burning of alien slash piles did however result

Table 5: Size distribution of seedlings per litre of soil from different post-fire treatments

Treatments	Seed size	Indigenous seedlings	Alien seedlings	Dead/Unidentified seedlings
Wildfire burnt fynbos	2–8mm	7.0 (1.8)	0.5 (0.5)	6.7 (3.0)
	1 000µm–2mm	39.2 (11.4)	0	9.2 (4.5)
	425–1 000µm	36.9 (7.8)	0	7.3 (4.9)
	<425µm	10.6 (3.9)	0	2.0 (1.3)
Wildfire burnt standing alien	2–8mm	2.6 (1.4)	5.4 (3.4)	2.1 (0.5)
	1 000µm–2mm	2.4 (0.8)	2.7 (1.8)	1.5 (0.9)
	425–1 000µm	3.7 (1.3)	0	1.7 (0.9)
	<425µm	3.0 (1.9)	0	1.0 (0.4)
	H	27.5	10.8	10.4
	P	0.0003	0.1462	0.1683
Wildfire burnt alien cleared fynbos	2–8mm	0	10.0	5.6
	1 000µm–2mm	41.5	0	13.3
	425–1 000µm	52.2	0	38.9
	<425µm	13.3	0	30.0
Wildfire burnt alien stacks	2–8mm	3.3	3.3	0
	1 000µm–2mm	0	0	4.4
	425–1 000µm	1.1	0	0
	<425µm	0	0	0

Figures in parentheses indicate standard errors of the means. Multiple Comparisons of the mean ranks for all seedling types in wildfire burnt fynbos vs wildfire burnt alien sites were calculated using the Kruskal-Wallis test (df = 7, n = 40). H = test statistic

Table 6: Total seedlings per litre of soil from different post-fire sites and from specific depth/size class combinations

Soil depth	Seed size	Treatments					
		Wildfire burnt fynbos	Wildfire burnt alien	U	P	Wildfire burnt alien cleared fynbos	Wildfire burnt alien stacks
0.00–0.02m	2–8mm	8.7 (4.2)	4.4 (2.8)	10	0.6905	10.0	10.0
	1 000µm–2mm	29.1 (8.2)	3.6 (2.2)	0	0.0079	4.4	0
	425–1 000µm	35.1 (16.0)	0.5 (0.5)	0	0.0079	13.3	3.3
	<425µm	7.2 (3.4)	0	5	0.1508	13.3	0
0.02–0.05m	2–8mm	9.1 (3.3)	10.6 (5.0)	11	0.8413	20.0	10.0
	1 000µm–2mm	56.0 (19.7)	9.2 (5.0)	2	0.0317	35.6	0
	425–1 000µm	53.1 (8.6)	1.2 (0.8)	0	0.0079	26.7	0
	<425µm	20.6 (8.1)	0.8 (0.8)	0	0.0079	13.3	0
0.05–0.15m	2–8mm	4.8 (3.2)	8.9 (4.1)	8.5	0.4206	0	0
	1 000µm–2mm	24.6 (9.4)	2.5 (1.6)	1	0.0317	84.4	0
	425–1 000µm	22.4 (5.1)	9.4 (3.4)	3.5	0.0555	116.7	0
	<425µm	4.1 (1.1)	8.2 (4.8)	11.5	0.8413	13.3	0

Figures in parentheses indicate standard errors of the means. Comparisons of the mean ranks of the wildfire burnt fynbos and wildfire burnt alien treatments were calculated using the Mann-Whitney U test. The valid n for both groups = 5

in good recruitment of indigenous reseeder species, confirming observations by Holmes (2001). This is probably explained by the less destructive, lower temperatures produced by fires during cooler, wetter months.

Our results show that fire intensity is a clear determinant of post-fire community structure. Heat scarred areas (under wildfire burnt stacks) are most affected by increasing fire intensity followed by burnt standing aliens, control burnt stacks, burnt cleared areas and burnt fynbos in that order. Of significance is the marked reduction in numbers of geophytes under alien stands and both geophytes and tussocks under wildfire burnt standing or stacked aliens.

An encouraging result of the field analyses was that indigenous species diversity in burnt cleared areas approximated that of the burnt fynbos after one year. This is indicative of a viable, persistent store of indigenous propagules under dense stands of woody alien plants. These findings agree with those of Holmes and Cowling (1997a, 1997b), Holmes and Richardson (1999), Holmes *et al.* (2000) and Holmes (2002), who described persistent indigenous soil seed banks in alien plant dominated Sandstone Fynbos communities. In this study however, buried indigenous propagules were largely destroyed by exceedingly hot fires in dense stands of living aliens and completely eliminated where stacks of alien slash were burnt by wildfires. The latent indigenous soil seed bank potential may therefore only be realised if alien biomass is removed from the area before hot summer burns occur.

Results of the nursery germination trial supported in-field findings; total counts showing parallel trends in terms of numbers of individuals per litre of soil and to a lesser extent, species richness. Total seed tray counts of indigenous seedlings decreased along a scale of increasing fire intensity. Burnt fynbos soils exhibited the highest total counts of indigenous seedlings. This is an expected result in fynbos, which is a fire prone ecosystem. Soils in burnt cleared areas have a strong indigenous component, despite having had a cover of alien species. Soils under burnt standing alien plants show much diminished numbers of seed of indigenous species and soils under stacks of wildfire burnt aliens exhibited almost no indigenous soil-stored seed banks.

The depth distribution of regenerating indigenous seedlings indicates that in areas dominated by pre-fire stands of alien plants, surface layers show depauperate amounts of indigenous seeds when compared to burnt Sandstone Fynbos. This may be a result of diminished seed rain from a reduced number of parent plants or a consequence of seed bank destruction by highly elevated burn intensities (evidently the reason in burnt standing aliens) (Holmes *et al.* 1997a). This is probably also the case in burnt cleared areas where seed banks are also diminished. Holmes' (2002) findings are supported here in that depauperate surface layers and deeply buried relictual indigenous seed banks are present under invaded alien stands in Sandstone Fynbos. The distribution of seed in wildfire burnt stack soils shows nearly entire elimination of all seeds, indigenous and alien, to depths up to and even exceeding 0.15m. Similarly, Milton and Hall (1981), Holmes *et al*. (1987) and Holmes (1989) note much reduced alien seed banks under stacks of wildfire burnt slash in fynbos habitats. At two out of three sites surveyed by Holmes *et al.* (1987), elimination of alien seed banks was complete. The depth distribution of post-fire soil seed banks of all species is therefore an important determinant of ensuing community composition.

Trends indicate that alien legume seeds (with the exception of *A. cyclops*) may be better able to survive higher fire intensities than their indigenous counterparts (Jeffery *et al*. 1988). Maximum germination of alien seedlings is from shallower soil depths in burnt standing alien infestations and in soil from burnt cleared areas. Possibly this is a consequence of one of the dominant standing alien species, *H. drupacea*, being serotinous and only releasing seed after being burnt. Another possible explanation being that improved fire survival is linked to larger seed size and the hard-seededness of alien legume species. The analysis of size-class distribution patterns of indigenous seedlings in soil from under burnt standing alien vegetation suggests that seed size has no influence on survival, while the distribution of seed in burnt cleared area soils were 'normal' (akin to the distribution in fynbos soils), except for elimination of the largest seed-size component (elimination of this component possibly being a stochastic effect of small sample size or more likely a result of indigenous pre-fire parent plant paucity and suppression by woody aliens (Holmes and Cowling 1997a)). Too few seeds survived in wildfire burnt stack soils to draw any valid statistical conclusions pertaining to size effects, barring the fact that one of five surviving seeds was a large seeded alien, *A. cyclops*. It is possible that the indigenous regeneration constituent (two *Lobelia* and two *Lepidium* plants) were ruderal. These findings do not support the findings of Musil and De Witt (1990) who established that seed size is an important determinant of post-fire regeneration in related Sand Fynbos on the lowlands. While seed size in Sandstone Fynbos may have some importance in determining fire survival in indigenous species, fynbos plants possibly rely more on the production of large numbers of small seeds to escape fire. As was the case in the field, the germination trials indicated that soil from wildfire burnt stacked areas are the worst affected by fires, followed by burnt standing aliens, burnt cleared areas and burnt fynbos habitats.

The January 2000 fires on the Cape Peninsula demonstrated the inability of authorities to control wildfires under extreme conditions. Large areas of alien and cleared vegetation remain vulnerable to runaway fires; therefore planning without introducing precautions to reduce the effects of runaway fires is unacceptable (Euston-Brown 2001). Considering the observed destructive effects of stacking and associated scarring, current management practices must be amended to reduce the negative effects of stacking, particularly as the unschooled labourers who undertake clearing have no background knowledge to avoid piling materials on rare or threatened plants or plant communities.

This paper shows that post-fire regeneration patterns, soil born seed-bank diversity and abundance are linked to pre-fire vegetation and seed characteristics of the component species. If the ultimate goal of alien plant management/eradication programmes is to restore the vegetation to its original state, then the current management practice of stacking is clearly incompatible with this ideal as is indicated by our field study and nursery germination trials. To ensure alien vegetation is managed to maximise the recruitment of native species, the following should be practised:

1. Alien vegetation should preferably not be cut and stacked,
2. If unavoidable, stack locations should be of low biological and aesthetic value, and
3. Stacks should be burnt during the winter to minimise damage.
4. Alternatively, other forms of management, such as winter burning of live alien stands, should be investigated further (see Holmes 1989, Holmes *et al.* 2000).

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